

## **ANALYSIS OF POWDERY MILDEW RESISTANCE IN THE SPANISH BARLEY CORE COLLECTION**

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## Abstract

The Spanish Barley Core Collection, consisting of one hundred and fifty-nine landrace-derived inbred lines and sixteen cultivars, was characterized for resistance to powdery mildew (*Blumeria graminis* f. sp. *hordei*) using a set of 27 isolates with a wide spectra of virulences/avirulences on most of the genes expected to occur in Europe. No landrace-derived line and no cultivar were resistant to all the isolates but at least 3 landraces showed infection types below 2 for 23 isolates. Twenty-two landraces and one cultivar showed resistance against half of the isolates used. Eleven isolates were sufficient to separate the majority of resistance profiles. In total, thirty-four resistance spectra were detected and fourteen resistance genes/alleles were postulated alone or in combination: *MiLa*, *Mlh*, *Mlg*, *Mla22*, *Mla7(Mlu)*, *Mla7(Mlk)*, *Mlk*, *Mla12*, *Mla9*, *Mla3*, *Mla6(Mla14)*, *Mlra* and *Mla1*. The majority of resistance spectra are composed only by one line. Resistance in twenty-one landrace-derived lines and four cultivars was based on either unidentified genes or combinations of known and unknown genes/alleles. Therefore, the SBCC may be a source for broadening the genetic base of powdery mildew resistance.

Key words: barley - core collection - disease resistance - powdery mildew - gene postulation

## Introduction

Powdery mildew caused by the biotrophic fungus *Blumeria graminis* f.sp. *hordei*, is one of the most destructive diseases of barley (*Hordeum vulgare* L.) in temperate latitudes worldwide. It is of great economic importance as it causes yield as well as seed quality losses (Zhang et al. 2005). The management of the disease normally involves the use of fungicides. However, their high cost, the environmental concerns and the insensitivity built up in the pathogen populations, have already led to a gradual limitation of their use in the past (Gullino and Kuijpers 1994). A cheaper and environment-friendly alternative to control this pathogen is the use of resistant cultivars. This option requires the knowledge of the genetics of mildew resistance in barley. Many resistance genes and quantitative trait loci (QTL) against powdery mildew have been identified in barley cultivars, landraces and wild *Hordeum* species (Friedt and Ordon 2007), and many of them have already been used in barley breeding in Europe (Brown and Jørgensen 1991). However, most of the genes commonly used by breeders are closely linked or allelic, which limits the number of gene combinations (Jørgensen 1994). Additionally, the continuous use of these genes often results in a selection in favour of pathotypes with the matching virulence genes in the pathogen population, and therefore in the 'breakdown' of the resistance. Only the *mlo* resistance gene has remained highly effective against powdery mildew for the last 30 years. During this period, it has been introgressed widely into two-rowed European spring barley cultivars. However, it has been scarcely used in winter barley breeding in Europe (Panstruga et al. 2005; Dreiseitl 2007). Therefore, new and effective resistance sources are still needed, especially for six-rowed winter barleys, which are grown widely in Southern Europe. For this purpose, tests for resistance must be carried out in order to identify genes or alleles conferring powdery mildew resistance in new cultivars or inbred lines. These tests are normally based on the gene-for-gene hypothesis (Flor 1971), which postulates that

for every gene in the plant that confers resistance, there is a corresponding gene in the pathogen conferring avirulence.

Landraces represent valuable reservoirs of genetic variability that may be utilized for gene and allele mining for disease resistance. Indeed, most of the powdery mildew resistance genes used commercially were derived from barley landraces (Fischbeck and Jahoor 1991). Large-scale cultivation of barley landraces in Europe practically ceased in the second half of the 20th century, with the advent of modern plant breeding. Currently, in most European countries, landraces exist only in gene banks (Ceccarelli et al. 2000) and they have not been fully exploited for resistances to powdery mildew. In Europe, attempts have been mostly conducted in Central and North-Western regions (Jensen et al. 1992, Caffier and de Vallavieille-Pope 1996, Dreiseitl and Jørgensen 2000). To our knowledge, few studies have been carried out in the European Mediterranean areas. Considering that the Fertile Crescent is assumed to be the original area of barley cultivation and North Africa one of the possible centres of barley diversification (Badr et al. 2000, Molina–Cano et al. 2002), we may speculate that barley landraces coming from Mediterranean regions may possess powdery mildew resistance genes different from those already identified in other European barleys. The Spanish Barley Core Collection (SBCC) (Igartua et al. 1998, Lasa 2008) comprises a representative sample of native landraces collected in Spain in the first half of the 20<sup>th</sup> century as well as some commercial cultivars successfully grown in Spain. Such landraces possess an important history of adaptation and selection under Mediterranean conditions which makes them a very attractive resource for new adaptive traits (Yahiaoui et al. 2008). Previous studies in the SBCC revealed the presence of significant levels of resistance to most frequently observed barley diseases, including powdery mildew (Silvar et al. 2010a). We can foresee that barley landraces collected from Spain may be a rich source of new genes for mildew resistance.

The main goals of this study were first, to evaluate these potentially new sources of resistances to *B. graminis* by analyzing the SBCC with a wide range of isolates possessing broad spectra of

virulences and second, to elucidate the putative resistance genes present in Spanish lines by comparing their infection types and resistance spectra with those of a differential set.

## **Material and methods**

**Plant materials.** The Spanish Barley Core Collection (Igartua et al. 1998), consisting of 159 (148 six-rowed and 11 two-rowed) inbred lines derived from local landraces, and 16 commercial cultivars (8 six-rowed and 8 two-rowed) with a long tradition of cultivation in Spanish agriculture was analyzed for powdery mildew resistance (the detailed composition of the collection can be consulted at <http://www.eead.csic.es/EEAD/barley/>).

A set of differential lines with known resistance genes was employed for gene postulation. It comprises 16 near-isogenic lines of 'Pallas' (Kølster et al. 1986) carrying genes *Mla1*, *Mla3*, *Mla6*, *Mla7*, *Mla9*, *Mla12*, *Mla13*, *Mla22*, *Mlra*, *Mlk*, *Mlat*, *Mlg*, *mlo5*, *MILa* and *Mlh*, seven European varieties with previously identified resistance genes *mlo9*, *Mlu*, *MI(Bw)*, *MI(He)*, *MI(Kr)*, *MI(Ab)* and *MI(St)* (Brown and Jørgensen 1991), six *Hordeum spontaneum* accessions or derived-lines possessing *Mlf*, *mlt*, *Mlj*, *Mla20*, *Mla27* and *Mla28* (Jahoor and Fischbeck 1987, 1993; Schönfeld et al. 1996), lines SI-1, SI-2, SI-5, SI-7, with unknown resistance and SI-6 (*Mlf+mlt*). The 34 differentials include most of the genes expected to occur in Europe (Brown and Jørgensen 1991). The susceptible variety 'Hanna' was used to control the inoculation efficiency. All barley plants were grown at 16 °C and continuous light (10,000 lux).

**Pathogen isolates.** Twenty-seven isolates of *B. graminis* f. sp. *hordei* held at the collection of the Julius Kühn-Institute in Kleinmachnow (Germany) were used. The names and origin of the isolates are shown in Table 1. The fungi were multiplied on leaf segments of the susceptible cv. 'Igri'.

**Resistance tests.** Eleven days after sowing, when the primary leaf was fully expanded, three leaf segments of 3 cm in length were excised from each line and placed adaxial surface up in a square Petri dish filled with 0.6% agar and 30 ppm benzimidazole. Inoculation was carried out by blowing

spores from the infected leaves over the leaf segments using a settling tower. A glass slide was placed in the settling tower to monitor inoculum density, which was adjusted to give approximately 2–4 conidia/mm<sup>2</sup>. About twelve days after inoculation, the infection types (IT) were recorded on a scale of 0–4 (including intertypes) following the procedure of Jahoor (1986). This scale was broadened by including an additional symbol 0(P) for IT characterised by only a few pustules on otherwise mildew free leaf segments, which is sometimes expressed when the *mlo* gene is present. Plants showing ITs 0-2 were classified as resistant and plants with ITs higher than 2 were included in the susceptible group.

**Data analysis and gene postulation.** Complexity and Gilmour Code of isolates were calculated using the HaGis Tool (Herrmann et al. 1999). The complexity of an isolate is defined as the number of differential lines which exhibit a disease reaction after infection with this isolate. The Gilmour method for the assignment of pathogen race names is based on an octal code for the designation of virulences/avirulences triplets (Gilmour 1973). Resistance complexity of each individual, determined as the number of negative responses (resistance) in its binary representation, and resistance frequency (RF), expressed as the proportion of individuals with a resistant reaction on each isolate from a given population, were analysed on the SBCC using the Virulence Analysis Tool (VAT) software (<http://www.uni-giessen.de/va-tipp>).

For gene postulation, all genotypes studied were compared with the differential set and those lines giving the same virulence/avirulence profile with all isolates were grouped into the same reaction spectrum (RS). Postulation of resistance genes was done on the basis of the gene-for-gene hypothesis (Flor 1971) known to be valid for the barley/powdery mildew system (Czembor and Czembor 2001). In the case of cultivars the hypothesis that a certain resistance gene is present in a host was further supported by using pedigree information, when available.

## Results

The twenty-seven isolates of *B. graminis* f. sp. *hordei* selected for this work displayed a broad spectrum of virulences (Table 1). All isolates were analyzed for complexity and Gilmour Code based on a set of 34 barley differential lines. The majority showed high complexity values, ranging from 25 (highly virulent) to 0 (avirulent) (Table 1). Fourteen isolates turned out to be virulent to more than 50% of the lines from the differential set. The highest complexity values were observed for isolates 78 and 75, which infected 25 and 24 barley differential lines, respectively. On the contrary, isolates 121 and 120 were avirulent for most lines tested, with complexities of 0 and 3, respectively (Table 1). The 27 isolates used in this study all showed different Gilmour codes based on the infections on the differential set. Therefore, they represent different pathotypes (Table 1).

The resistance complexity analysis of the 159 barley landrace-derived SBCC lines showed that 151 (ca. 95%) resisted to at least one isolate of *B. graminis* f. sp. *hordei* and twenty-two lines (13.8%) were resistant to 50% of the isolates used (Fig. 1). About 17.2% of all reaction types were classified as powdery mildew resistant (scores 0, 1 and 2) (Fig. 2). Some IT scores 0(P), characteristic for the resistance gene *mlo*, were detected (Fig. 2). No line was resistant to all isolates, but at least 3 landrace-derived lines (SBCC097, SBCC141 and SBCC145) displayed a wide spectrum of resistance, with an IT score  $\leq 2$  for 23 isolates. Resistance of SBCC097 was characterized by an infection type 0(P) to several isolates, whereas lines SBCC141 and SBCC145 showed a combination of infection types 0, 1 and 2 (data not shown). Fifteen cultivars showed resistance after inoculation with at least one of the isolates tested but only one cultivar showed resistance after infection with half of the isolates tested. The most resistant cultivar was 'Kym' (SBCC171) which was susceptible only to six *B. graminis* isolates. Eight landraces (5%) and none of the cultivars were susceptible to all isolates. Mean scores of 2.84 and 2.83 for landraces and cultivars, respectively, indicated no differences in overall resistance levels between them. Isolates 75 and 170 were the most virulent on the SBCC (RF=0.051), whereas isolate 121 had the lowest levels of infection (RF=0.94).

Isolates that recognized at least one known resistance gene on the barley differential lines, i.e. they are avirulent, were selected for gene postulation. When different isolates recognized the same resistance genes, those with the higher complexity were chosen. Gene postulation was performed following two steps: firstly, eliminating resistance genes not present in the tested lines and secondly, postulating the resistance genes/alleles. Eleven isolates of *B. graminis* were sufficient to separate all different reaction spectra (RS) on the differential set. Patterns of virulence/avirulence of these isolates allowed identifying up to 30 resistance genes/alleles on the barley differential lines (Table 2). Conclusions about the putative presence of known genes in the SBCC were made by comparing the RS of these eleven isolates in the tested lines (SBCC landraces and cultivars) with those expressed by differential lines. Based on these data, it was possible to distinguish 34 different RS in the SBCC (Table 3). Landrace-derived lines were grouped into RS from 1 to 32. RS1 consists of all lines without any effective resistance gene based on this set of eleven isolates, i.e., all isolates produced IT above 2 on these lines. On the contrary, RS31 (SBCC097) and RS32 (SBCC145) include genotypes with resistance to ten and eleven isolates, respectively. Twenty-one RS comprise only one accession and the majority of lines were grouped in RS1 (50.2%).

Resistance genes/alleles could be postulated for 38 landrace-derived lines and seven cultivars. It was not possible to postulate which resistance genes/alleles are present in 41 landrace-derived lines (Table 3). Fourteen different resistance genes/alleles were postulated to be present in the rest of the lines, alone or in combination: *MILa*, *Mlh*, *Mlg*, *Mla22*, *Mla7(Mlu)*, *Mla7(Mlk)*, *Mlk*, *Mla12*, *Mla9*, *Mla3*, *Mla6(Mla14)*, *Mlra* and *Mla1*. The most common alleles were *MILa*, *Mlh* and *Mlg*, which appeared in 14 (8%), 10 (5.7%) and 8 (4.5%) accessions, respectively. RS2 to RS6 were conditioned by the gene *MILa* alone or combined with unidentified genes. RS9-RS14 included lines with the gene *Mlh* alone or in combination. RS15-RS18 comprised accessions with *Mlg* alone or in combination with other genes. Gene *Mla7* (alone or in combination) conditions the resistance of spectra RS20-RS25 (Table 3).



Cultivars were mostly grouped on RS numbers 1 and 15 and there are two RS (RS33 and RS34) that consist of only one cultivar. The most common genes in cultivars were *Mlg* and *Mlh* which were postulated in four and two cultivars, respectively (Table 4). In eight cultivars it was not possible to identify any effective gene with the set of eleven isolates. Information on pedigree, when available, was employed to confirm postulated genes.

Unidentified or unknown resistances in combination with known resistance alleles were suspected in sixteen RS which comprise nineteen landrace-derived lines (12%) and three cultivars (18.8%). No differences were observed regarding predicted genes between landrace-derived inbred lines and cultivars or between winter/spring and two/six-rowed cultivars.

The set of eleven isolates selected for gene postulation could not disclose the resistance present in 80 landrace-derived lines and 8 cultivars (RS1). Most presented resistances to a few of the isolates left out of the diagnostic panel (only 8 out of them were susceptible to all 27 isolates), and their overall resistance level was quite low.

## **Discussion**

A wide-array of *B. graminis* f. sp. *hordei* pathotypes with broad spectra of virulence was used for resistance tests. These isolates collectively represented virulence to most major resistance genes used in Europe. Among 159 landrace-derived lines investigated, 22 (ca. 14%) showed resistance to more than 50% of the isolates used. These percentages of resistance seem smaller than those observed in other studies performed on landrace collections (Jørgensen and Jensen, 1997; Czembor, 2000; Czembor and Czembor, 2000), although variations in methods and isolates used for screening among the different studies make comparisons difficult.

Three landrace-derived lines turned out to be highly resistant, against 23 isolates (SBCC097, SBCC141 and SBCC145). Resistance of line SBCC097 was characterized by infection type 0(P) to several isolates. This IT is often expressed in barleys with *mlo* resistance. However, susceptibility

of this line to isolates 120, 125, 126 and 179, which are avirulent on P22 (*mlo5*) and Alexis (*mlo9*), indicates that *mlo* is not responsible for the resistance of this line. Additional evidences for a non-based *mlo* resistance were found in molecular analyses (Silvar et al. 2010b). Lines SBCC141 and SBCC145 showed a combination of infection types 0, 1 and 2, which suggests that they might carry more than one resistance gene, as it has been reported in similar studies (Czembor 2002, Dreiseitl and Bockelman 2003). Interestingly, these three lines showed distinctive RS to the 23 isolates, i.e., they are not infected by the same isolates. This suggests the presence of different gene combinations and points to the potentially high diversity of the SBCC regarding powdery mildew resistance.

The distribution of resistant infection type scores normally gives an idea about the minimum number of genes involved, since different genes for resistance may condition different reaction types (0, 1 or 2) (Czembor 1999). The majority of powdery mildew resistance genes used in Europe confers mostly infection types 0 and 1 (Brown and Jørgensen 1991). Five landrace-derived lines (SBCC014, SBCC036, SBCC042, SBCC058 and SBCC141) and cv. 'Kym' (SBCC171) presented this type of reaction after inoculation with up to 13 isolates. Indeed, these accessions are included in RS25, 26 and 27 where known resistance genes/alleles were postulated. This suggests that these lines might possess mainly resistances already described in Europe. Infection type 2 to a wide range of isolates was frequent in our work (28.2%). This usually indicates partial resistance to powdery mildew (Czembor and Gacek 1995).

The RS spectra and IT inferred by any of the landrace-derived lines and cultivars were compared with those of the differential set after simultaneous infection type readings. Eleven *B. graminis* pathotypes were sufficient to distinguish 30 genes/alleles on the differential set as well as to separate the major resistance spectra. The addition of more isolates would increase the number of RS but it would not provide any additional information on the genes/alleles present in tested lines. Similar conclusions have been driven in similar works (Dreiseitl and Jørgensen 2000, Dreiseitl and Rashal 2004, Dreiseitl and Yang 2007).

The most common alleles in the SBCC were *MiLa*, *Mlh*, *Mlg*, *Mla6* and *Mla7*. The genes *MiLa* (resistance 'Laevigatum') and *Mlg* (resistance 'Weihenstephan') have been the most widely used in European barley breeding (Brown and Jørgensen, 1991). The absence of linkage between *MiLa* (2H) and *Mlg* (4H) (Chelkowski et al. 2003, Korell et al. 2008) facilitated their use in combination. These two genes, together with *Mlh* (from 'Hauters') were among the first genes widely introduced in Europe, especially in winter barley (Brown and Jørgensen 1991). Nowadays, they are "defeated" genes and virulences to *La*, *g* and *h* have been commonly reported in powdery mildew populations from North Africa and Europe (Yahyaoui et al. 1997, Høvmøller et al. 2000).

The most frequent *Mla* alleles in European cultivars are *Mla7*, *Mla12*, *Mla6* and *Mla3*. All were postulated in Spanish barleys, although *Mla7* and *Mla6* were the most common ones. *Mla7* (named after 'Lyallpur') was originally described in landraces from the Indian subcontinent and was also detected in landraces from China (Jørgensen 1994, Dreiseitl and Yang 2007). The *Mla6* allele (from '*H. spontaneum*') was cloned by Halterman et al. (2001) and it confers a rapid defence response phenotype. *Mla14* is often postulated to be very similar to *Mla6*, and for this reason we kept the nomenclature as *Mla6(Mla14)*. Interestingly, the alleles *MiLa*, *Mlh*, and *Mla7* have not been commonly described in landrace material. On the contrary, genes *Mlg*, *Mla6*, *Mlk*, *Mla1* and *Mla12*, which were identified in the Spanish barleys, were also detected in landraces from Tunisia, Morocco, Jordan and Greece (Czembor 1999, 2000, 2001; Czembor and Czembor, 1999). All these countries belong to the Mediterranean region. Co-evolution between powdery mildew populations and landraces from different countries might result in the presence of common resistance alleles in the Mediterranean areas. Curiously, we could not identify other alleles, such as *Mlat* ('Atlas'), which were originally described in germplasm from North Africa (Jørgensen 1994) and have been frequently reported in landraces coming from Morocco, Jordan and Greece, (Czembor and Czembor 1999, 2000; Czembor 2001). In the same way, we did not detect any of the *Mi*-genes: *a20*, *a27*, *a28*, *f*, *j* or *t*, even though they could have been identified with the differential set used. These genes were

all derived from *H. spontaneum* accessions collected in the Mediterranean region (primarily from Israel) (Jahoor and Fischbeck 1987, 1993; Schönfeld et al. 1996). Some wild barley lines carrying *Mla16*, *a17*, *a18*, *a19* and *a26* genes were also included in the differential set during the experimental work. They were subsequently discarded for the differential set due to the absence of compatible reactions (susceptibility) with the 27 isolates used (data not shown). The absence of isolates coming from the same regions as these *H. spontaneum* sources in our panel of isolates might explain this result, as it was observed in other studies (Dreiseitl and Dinooor 2004).

Powdery mildew resistance genes present in cultivars did not differ from those in landrace-derived lines. This is not surprising considering that some of the cultivars originated from local landraces. Whenever possible, the alleles inferred on the cultivars were confirmed by tracing the resistance genes in pedigrees. The Cereal Pathogen Resistance Allele Database (<http://cprad.scri.ac.uk>) (CPRAD) hosted at the Scottish Crop Research Institute website, was employed to check the pathogen resistance alleles that have been previously reported in several barley genotypes. Cultivars from the SBCC were grouped in 6 different RS and five different resistance genes/alleles were postulated. The spring two-rowed British cultivar 'Kym' (SBCC171) showed the highest level of resistance among the cultivars. We established the presence of *Mla9* in this variety in combination with *Mlg* and *MILa*, which is in agreement with Brown and Jørgensen (1991) and with data available at the CPRAD catalogue. Resistance gene *Mlg* was also postulated in other three cultivars. Two of these, 'Dobla' (SBCC164) and 'Zaida' (SBCC175) share the parent 'Union' in their pedigree, which contains the *Mlg* gene. Additional genes (*Mla7* and *Mlk*) of the parental lines ('Nymphé' and 'Adorra') were not detected in our cultivars. For cv. 'Alpha', it was not possible to find out the resistance genes present on its pedigree information (Ager×(Ager×Ceres)). Caffier and Vallavieille-Pope (1996) did not find any specific resistance in the French cultivar 'Barbarrousse'. *MILa* was suggested for this cultivar in our test, but unfortunately, there is no information on the resistance of 'Hatif de Grignon' and 'Ares', which might be the donors of this gene. The gene *Mlh*

was postulated in cv. 'Hassan', but none of the respective parents contains this gene. On the contrary, according to the CPRAD catalogue, this cultivar possess the *Mla12* allele (from 'Arabische'), which was not identified in our experiments. No gene was identified in Spanish cultivars derived from local landraces using these eleven isolates, except for 'Panél', in which *Mlh* was inferred.

Previous tests on the SBCC (Silvar et al. 2010a) carried out with a lower number of isolates, revealed slightly higher levels of resistance to powdery mildew than found in this study. These former experiments were carried out in greenhouse assays on potted plants, whereas the results presented here come from tests performed on detached leaves assays. There are two reasons that could explain these differences. The first, and most important one, is the existence of differences among the isolates. The set of isolates used in previous studies possessed a narrow virulence spectrum compared to the group of isolates employed in this study. We used only three common isolates (78, 79 and 126) and data on these were very similar in both experiments. The second explanation is the severity of infection, which is always higher on the detached leaves experiments due to a higher density of inoculum, in comparison to greenhouse tests.

The most remarkable aspect of this work is the diversity detected in the SBCC regarding powdery mildew resistance. The majority of resistance spectra are composed only by one line and in several lines the presence of unknown genes alone or in combination with known genes was postulated. Presence of a high number of unknown genes in barley landraces is in agreement with findings from other studies (Jørgensen and Jensen 1997, Czembor and Czembor 1999, Czembor 2000). Studies on bi-parental populations derived from the most resistant lines supports such variability. Landrace derived line SBCC097 (Silvar et al. 2010b) possesses a resistance totally different from the line SBCC145 (unpublished data), and, in both cases, they seem to represent potentially new alleles or loci distinct from the ones described so far. From our point of view, the great value of Spanish

landraces as sources of new resistances against powdery mildew lies mainly in these uncharacterised resistances, than in the inferred genes.

Obviously, further investigation in the SBCC will be needed to confirm the postulated resistance genes as well as to investigate the unknown resistances, which may be influenced by different levels of partial or quantitative resistance. Nevertheless, preliminary results in this paper suggest that some Spanish landraces may significantly contribute to the diversification of powdery mildew resistance gene pools used in breeding programmes.

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**Table 1.** Name, origin, complexity and Gilmour Code for the twenty-seven *B. graminis* f. sp. *hordei* isolates used in this work based on a set of 34 differential barley lines.

| <b>Isolate</b> | <b>Origin</b> | <b>Complexity</b> | <b>Gilmour Code</b> |
|----------------|---------------|-------------------|---------------------|
| 75             | Denmark       | 24                | 77777457640         |
| 78             | Denmark       | 25                | 77773357650         |
| 79             | Austria       | 21                | 77773741240         |
| 82             | Austria       | 19                | 77777541000         |
| 114            | Denmark       | 9                 | 57506000000         |
| 116            | Denmark       | 8                 | 67064000000         |
| 118            | Denmark       | 7                 | 72114000000         |
| 120            | Denmark       | 3                 | 40005000000         |
| 121            | Denmark       | 0                 | 00000000000         |
| 122            | Denmark       | 8                 | 72106040000         |
| 125            | Denmark       | 18                | 77753061240         |
| 126            | Denmark       | 14                | 77674420000         |
| 127            | Denmark       | 16                | 77652541200         |
| 164            | Germany       | 15                | 77774600000         |
| 167            | Germany       | 12                | 77724000400         |
| 168            | Germany       | 16                | 77632316000         |
| 170            | Germany       | 19                | 77775620410         |
| 176            | Germany       | 20                | 77773061640         |
| 178            | Germany       | 20                | 75773716010         |
| 179            | Germany       | 14                | 77740200130         |
| 180            | Germany       | 19                | 75775336000         |
| 199            | Sweden        | 20                | 77772716400         |
| 211            | Sweden        | 23                | 77772777100         |
| 212            | Sweden        | 20                | 77776716000         |
| 221            | Germany       | 17                | 77775400120         |
| 224            | Germany       | 18                | 77755020126         |
| 225            | Germany       | 18                | 77763420124         |

**Table 2.** Infection types of eleven selected isolates of *B. graminis* f. sp. *hordei* on a differential set of 34 barley lines.

| Accession  | Gene                  | Code <sup>1</sup> | <i>B. graminis</i> f. sp. <i>hordei</i> isolates |      |      |      |     |     |      |     |      |      |     |
|------------|-----------------------|-------------------|--|------|------|------|-----|-----|------|-----|------|------|-----|
|            |                       |                   | 75   | 114  | 116  | 122  | 127 | 168 | 170  | 179 | 180  | 211  | 224 |
| P01        | <i>Mla1</i>           | Al                | 1  | 0    | 0    | 0    | 0   | 1   | 0    | 2-3 | 0    | 3    | 3   |
| P02        | <i>Mla3</i>           | Ri                | 2  | 1    | 1    | 1-2  | 1   | 2   | 4    | 1-2 | 2-3  | 3    | 3   |
| P03        | <i>Mla6, (Mla14)</i>  | Sp                | 4  | 2    | 3    | 0    | 0   | 4   | 4    | 0   | 3    | 3    | 0   |
| P04B       | <i>Mla7, Mlu</i>      | Ly,u              | 4  | 2-3  | 2    | 1-2  | 3   | 4   | 4    | 2-3 | 3    | 4    | 3   |
| P06        | <i>Mla7, (Mlk)</i>    | Ly                | 4  | 1    | 1    | 1    | 3   | 4   | 3    | 2-3 | 3    | 3    | 3   |
| P08B       | <i>Mla9</i>           | MC                | 4  | 1    | 0    | 3    | 3   | 0   | 0    | 0   | 0    | 3    | 0   |
| P10        | <i>Mla12</i>          | Ar                | 4  | 2-3  | 1    | 4    | 1   | 2   | 2-3  | 2-3 | 3    | 3    | 3   |
| P11        | <i>Mla13, Ml(Ru3)</i> | Ru                | 1  | 1    | 0    | 0    | 4   | 4   | 1    | 0   | 3    | 3    | 0   |
| P12        | <i>Mla22</i>          | -                 | 4  | 3    | 3    | 3    | 0   | 0   | 3    | 0   | 3    | 0    | 4   |
| P14        | <i>Mlra</i>           | Ra                | 4  | 3-4  | 3    | 1    | 4   | 4   | 4    | 3   | 3    | 4    | 4   |
| P17        | <i>Mlk</i>            | Kw                | 4  | 4    | 1    | 4    | 4   | 4   | 2    | 1-2 | 2    | 3    | 2   |
| P20        | <i>Mlat</i>           | At                | 2-3  | 2    | 1-2  | 2    | 2   | 2   | 3    | 2   | 3    | 2    | 4   |
| P21        | <i>Mlg, (Ml(CP))</i>  | We                | 4  | 0    | 3    | 0    | 3   | 0   | 4    | 3   | 3    | 3    | 4   |
| P22        | <i>mlo5</i>           | -                 | 0  | 0    | 0(P) | 0    | 0   | 0   | 0(P) | 2   | 0    | 0(P) | 0   |
| P23        | <i>MILa</i>           | La                | 4  | 3    | 2-3  | 2-3  | 4   | 2-3 | 3    | 3   | 2    | 3    | 4   |
| P24        | <i>Mlh</i>            | Ha                | 3-4  | 0(P) | 3    | 4    | 4   | 4   | 3    | 3   | 4    | 3    | 4   |
| Alexis     | <i>mlo9</i>           | -                 | 0(P)   | 0    | 0    | 0    | 0   | 0   | 0(P) | 0   | 0(P) | 0(P) | 0   |
| Banteng    | <i>Mlu</i>            | -                 | 4  | 3    | 2-3  | 1    | 3   | 4   | 3    | 3   | 3    | 3    | 4   |
| Borwina    | <i>Ml(Bw)</i>         | -                 | 4  | 2-3  | 0(P) | 3    | 2-3 | 3   | 3    | 3   | 3    | 3    | 3   |
| Hellas     | <i>Ml(He)</i>         | -                 | 4  | 4    | 3    | 4    | 4   | 4   | 4    | 3   | 3    | 4    | 4   |
| Kredit     | <i>Ml(Kr)</i>         | -                 | 3  | 1-2  | 1-2  | 2    | 3   | 4   | 3    | 2   | 3    | 3    | 2-3 |
| Lotta      | <i>Ml(Ab)</i>         | -                 | 0  | 0(P) | 0(P) | 0(P) | 0   | 3   | 3    | 2-3 | 3    | 3    | 1   |
| Steffi     | <i>Ml(St)</i>         | -                 | 2-3  | 0    | 0    | 0    | 4   | 2   | 3    | 1   | 2    | 3    | 2   |
| HSY-78*A   | <i>Mlf</i>            | -                 | 3  | 1    | 0    | 1    | 0   | 2-3 | 1-2  | 0   | 2-3  | 3    | 0   |
| RS137-28*E | <i>Mlj</i>            | -                 | 2-3  | 2    | 0    | 1    | 0   | 2   | 2-3  | 0   | 1-2  | 1-2  | 0   |
| RS42-6*O   | <i>Mlt</i>            | -                 | 4  | 2    | 0    | 0    | 0   | 3   | 2    | 0   | 3    | 2-3  | 0   |
| RS-145-39  | <i>Mla20</i>          | -                 | 1  | 0    | 0    | 0    | 0   | 0   | 2    | 0   | 0    | 2    | 2-3 |
| RS-1-8     | <i>Mla27</i>          | -                 | 0  | 0    | 0    | 0    | 0   | 1   | 0    | 2-3 | 0    | 2    | 4   |
| 1B-151     | <i>Mla28</i>          | -                 | 3  | 1    | 0    | 1    | 0   | 3   | 1    | 0   | 2-3  | 3    | 0   |
| SI-1       | <i>Ml(SI-1)</i>       | -                 | 0  | 0    | 0    | 0    | 0   | 0   | 0    | 0   | 0    | 1    | 3   |
| SI-2       | <i>Ml(SI-2)</i>       | -                 | 1  | 0    | 0    | 0    | 0   | 0   | 2-3  | 2-3 | 2    | 0    | 2   |
| SI-5       | <i>Ml(SI-5)</i>       | -                 | 4  | 0    | 0    | 1    | 3   | 0   | 1    | 0   | 0    | 3    | 0   |
| SI-6       | <i>Mlf, mlt</i>       | -                 | 3  | 0    | 0    | 2    | 2   | 0   | 0    | 0   | 0    | 1-2  | 0   |
| SI-7       | <i>Ml(SI-7)</i>       | -                 | 2-3  | 1    | 0    | 2    | 2-3 | 0   | 0    | 0   | 0    | 2    | 0   |

<sup>1</sup>Anonymous 1991

**Table 3.** Resistance spectra and postulated resistance genes/alleles in 159 landrace-derived inbred lines from the SBCC to infection by eleven selected isolates of *Blumeria graminis* f.sp. *hordei*

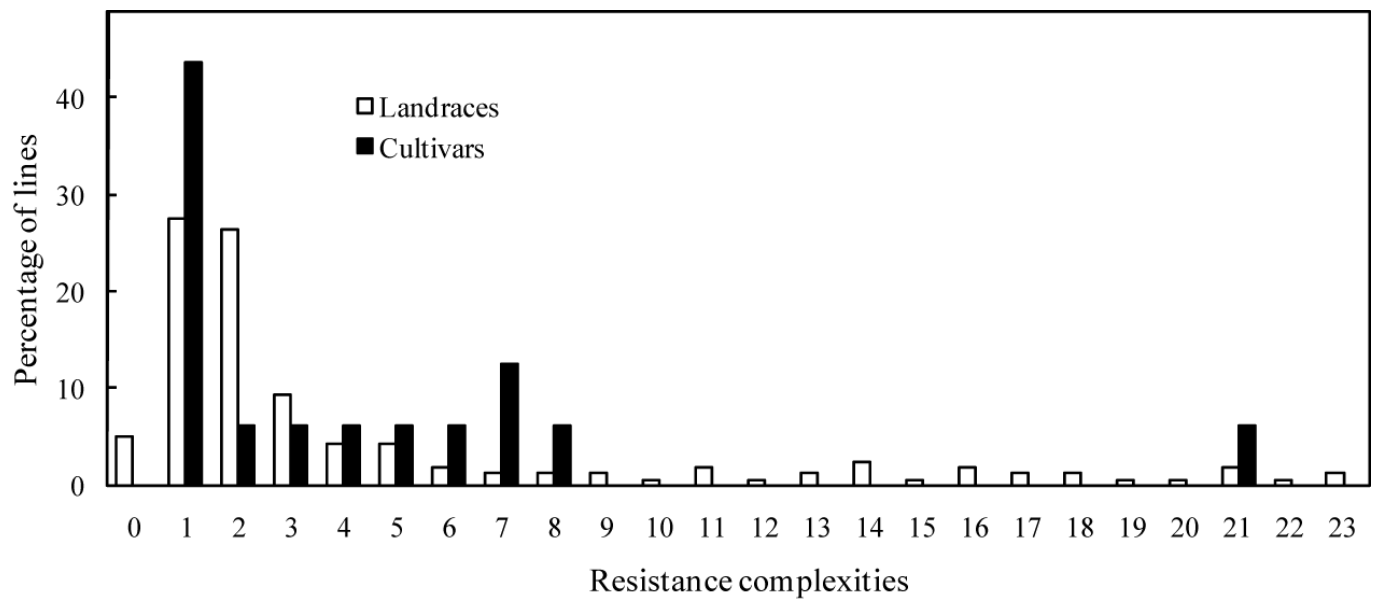
| RS | N° lines | <i>B. graminis</i> f.sp. <i>hordei</i> isolates |      |     |     |      |     |      |     |      |      |     | Postulated Genes                   | Code <sup>1</sup> |
|----|----------|---|------|-----|-----|------|-----|------|-----|------|------|-----|------------------------------------|-------------------|
|    |          | 75  | 114  | 116 | 122 | 127  | 168 | 170  | 179 | 180  | 211  | 224 |                                    |                   |
| 1  | 80       | 4   | 3    | 3   | 3   | 4    | 3   | 3    | 2-3 | 4    | 3    | 4   | <i>None</i>                        | -                 |
| 2  | 4        | 3   | 3    | 3   | 3-4 | 3-4  | 3   | 3-4  | 3   | 1    | 3    | 3   | <i>MLa</i>                         | La                |
| 3  | 1        | 3-4   | 3    | 3-4 | 3   | 3-4  | 3-4 | 3    | 0-1 | 1    | 3    | 2-3 | <i>MLa, ?</i>                      | La                |
| 4  | 3        | 3-4   | 3    | 3   | 3   | 0(P) | 3   | 3-4  | 0   | 0(P) | 3    | 3   | <i>MLa, ?</i>                      | La                |
| 5  | 1        | 4   | 2-3  | 2-3 | 3   | 0(P) | 2-3 | 2-3  | 0   | 0    | 0(P) | 2-3 | <i>MLa, ?</i>                      | La                |
| 6  | 1        | 3   | 2-3  | 2-3 | 3   | 0(P) | 2-3 | 3    | 0   | 0    | 2    | 2   | <i>MLa, ?</i>                      | La                |
| 7  | 1        | 3   | 2-3  | 2-3 | 2   | 2    | 3   | 3    | 0   | 3    | 2-3  | 4   | <i>Mlra, ?</i>                     | Ra                |
| 8  | 1        | 2-3   | 2-3  | 2-3 | 2-3 | 0(P) | 2   | 3    | 0   | 2    | 2    | 3   | <i>MLa, Mla22</i>                  | La                |
| 9  | 2        | 3-4   | 0-1  | 3   | 3   | 4    | 3-4 | 3-4  | 3   | 4    | 3-4  | 4   | <i>Mlh</i>                         | Ha                |
| 10 | 1        | 2-3   | 2    | 2-3 | 2-3 | 2    | 2-3 | 2-3  | 2-3 | 4    | 3    | 4   | <i>Mlh, ?</i>                      | Ha                |
| 11 | 1        | 3   | 2    | 3   | 3   | 3    | 3   | 3    | 0   | 3    | 3    | 4   | <i>Mlh, ?</i>                      | Ha                |
| 12 | 1        | 2-3   | 0(P) | 2   | 2-3 | 1    | 3   | 2-3  | 1   | 3    | 2-3  | 3   | <i>Mlh, ?</i>                      | Ha                |
| 13 | 1        | 2-3   | 1    | 2-3 | 2-3 | 2    | 2   | 3    | 2-3 | 2    | 2    | 2-3 | <i>Mlh, MLa, ?</i>                 | Ha, La            |
| 14 | 2        | 3   | 2    | 1-2 | 3   | 2    | 3   | 2-3  | 0   | 1    | 1-2  | 2   | <i>Mlh, MLa, ?</i>                 | Ha, La            |
| 15 | 2        | 4   | 0    | 3   | 0   | 4    | 0   | 3-4  | 3   | 3-4  | 3-4  | 3-4 | <i>Mlg</i>                         | We                |
| 16 | 1        | 2   | 0(P) | 2-3 | 2   | 0    | 2   | 2    | 0   | 4    | 3    | 4   | <i>Mlg, ?</i>                      | We                |
| 17 | 1        | 3   | 0    | 2-3 | 0   | 0    | 2   | 3    | 2   | 4    | 1    | 1   | <i>Mlg, Mla22, Mla6(Mla14)</i>     | We, Sp            |
| 18 | 1        | 1   | 0    | 4   | 0   | 0    | 1   | 4    | 0   | 4    | 0    | 1   | <i>Mlg, Mla22, Mla6(Mla14), ?</i>  | We, Sp            |
| 19 | 2        | 3   | 2-3  | 2   | 2   | 0-1  | 3   | 2-3  | 0   | 3-4  | 3    | 2   | <i>Mla7(Mlu), Mla6(Mla14)</i>      | Ly, u, Sp         |
| 20 | 1        | 3   | 3    | 0   | 1   | 0(P) | 2-3 | 2    | 0   | 1    | 3    | 1   | <i>Mla7(Mlu), Mlk, ?</i>           | Ly, u, Kw         |
| 21 | 1        | 2   | 2-3  | 1   | 2   | 2    | 2   | 2-3  | 3   | 4    | 2    | 3   | <i>Mla7(Mlu), Mla12, ?</i>         | Ly, u, Ar         |
| 22 | 2        | 3   | 0    | 0-1 | 1   | 0(P) | 3   | 3    | 0   | 3-4  | 3    | 0   | <i>Mla7(Mlk), Mla6(Mla14)</i>      | Ly, Sp            |
| 23 | 1        | 2   | 2    | 2   | 2   | 2    | 2-3 | 2-3  | 3   | 3    | 2    | 4   | <i>Mla7(Mlk), ?</i>                | Ly                |
| 24 | 1        | 2-3   | 2    | 2   | 2   | 2    | 2-3 | 2-3  | 3   | 0(P) | 2    | 3   | <i>Mla7(Mlk), MLa, ?</i>           | Ly, La            |
| 25 | 1        | 3-4   | 0    | 0   | 1   | 0    | 3   | 0    | 0   | 0    | 3    | 0   | <i>Mla7(Mlk), Mlk, Mla6(Mla14)</i> | Ly, Kw, Sp        |
| 26 | 1        | 1   | 0    | 0   | 0   | 0    | 1   | 2-3  | 0   | 3    | 2    | 2   | <i>Mla3, Mla6(Mla14), Mla22</i>    | Ri, Sp            |
| 27 | 3        | 0   | 0    | 0   | 0-1 | 0    | 0-1 | 0-1  | 3   | 0    | 3-4  | 4   | <i>Mla1</i>                        | Al                |
| 28 | 1        | 3-4   | 3    | 3   | 2-3 | 2    | 3   | 3    | 0   | 3    | 2-3  | 2-3 | <i>?</i>                           | -                 |
| 29 | 2        | 2-3   | 2-3  | 3   | 3   | 0(P) | 2-3 | 2-3  | 2-3 | 2-3  | 3    | 3   | <i>?</i>                           | -                 |
| 30 | 36       | 3   | 3    | 3   | 3   | 3    | 3   | 3    | 0-1 | 4    | 2-3  | 4   | <i>?</i>                           | -                 |
| 31 | 1        | 1   | 0(P) | 0   | 1-2 | 2    | 2   | 0(P) | 2-3 | 0(P) | 2    | 2   | <i>?</i>                           | -                 |
| 32 | 1        | 2   | 0    | 1-2 | 0   | 0    | 1   | 0    | 0   | 2    | 0    | 0   | <i>?</i>                           | -                 |

<sup>1</sup>Anonymous 1991

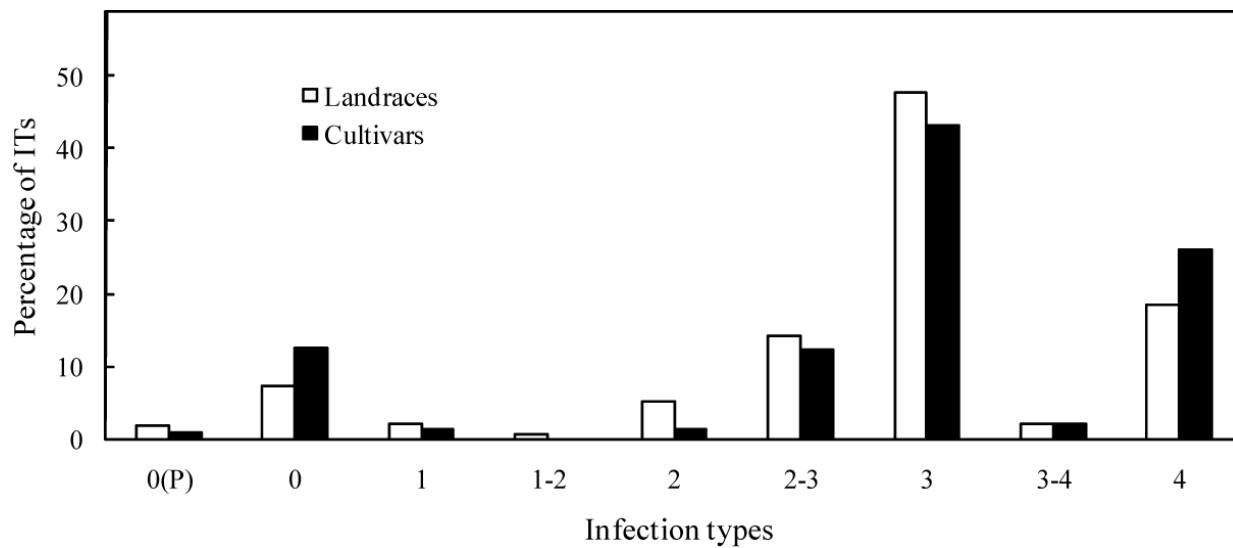
**Table 4.** Resistance spectra and postulated resistance alleles in 16 cultivars from the SBCC to infection by eleven selected isolates of *Blumeria graminis* f.sp. *hordei*

| Name    | Cultivar         | Description          | Origin        | Pedigree                                    | RS | Postulated genes       | Code <sup>1</sup> |
|---------|------------------|----------------------|---------------|---|----|------------------------|-------------------|
| SBCC160 | Ager             | winter, 6-rowed      | France        | (Bordia x Kenia) × Weihenstephan 259-711    | 1  | <i>None</i>            | -                 |
| SBCC161 | Albacete         | facultative, 6-rowed | Spain         | Spanish selection from local landrace       | 1  | <i>None</i>            | -                 |
| SBCC162 | Almunia          | winter, 6-rowed      | Spain         | Spanish selection from local landrace       | 1  | <i>None</i>            | -                 |
| SBCC163 | Barberousse      | winter, 6-rowed      | France        | (Hauter × (Hatif de Grignon x Ares)) × Ager | 3  | <i>MILa,?</i>          | La                |
| SBCC164 | Dobla            | winter, 6-rowed      | Spain         | Union × Nymphe                              | 15 | <i>Mlg</i>             | Ha                |
| SBCC165 | Hatif de Grignon | winter, 6-rowed      | France        | French selection from local landrace        | 1  | <i>None</i>            | -                 |
| SBCC166 | Monlon           | winter, 6-rowed      | France        | Breustedt Schladener × Hatif de Grignon     | 1  | <i>None</i>            | -                 |
| SBCC167 | Panel            | facultative, 6-rowed | Spain         | Spanish selection from local landrace       | 11 | <i>Mlh,?</i>           | Ha                |
| SBCC168 | Alpha            | winter, 2-rowed      | France        | Ager × (Ager × Ceres)                       | 15 | <i>Mlg</i>             | We                |
| SBCC169 | Beka             | spring, 2-rowed      | France        | Bethge XIII × Kneifel                       | 1  | <i>None</i>            | -                 |
| SBCC170 | Hassan           | spring, 2-rowed      | Holland       | Delta × (Agio × Kenia 3 × Arabische)        | 33 | <i>Mlh,?</i>           | Ha                |
| SBCC171 | Kym              | spring, 2-rowed      | Great Britain | Georgie × Hanna                             | 34 | <i>Mlg, MILa, Mla9</i> | We, La, MC        |
| SBCC172 | Pallas           | spring, 2-rowed      | Sweden        | Mutant derived from Bonus                   | 30 | <i>?</i>               | -                 |
| SBCC173 | Trait d'Union    | spring, 2-rowed      | France        | Weih. Melh II × Firlbeck 621                | 1  | <i>None</i>            | -                 |
| SBCC174 | Wissa            | spring, 2-rowed      | Germany       | (Weih. Melh. I × Breun IN 2511) × Isaria    | 1  | <i>None</i>            | -                 |
| SBCC175 | Zaida            | spring, 2-rowed      | Spain         | Adorra × Union                              | 15 | <i>Mlg</i>             | We                |

<sup>1</sup>Anonymous 1991



**Figure 1.** Distribution of resistance complexities observed for cultivars and landrace-derived inbred lines from the SBCC based on twenty-seven isolates of *B. graminis* f. sp. *hordei*.



**Figure 2.** Distribution of infection types observed for cultivars and landrace-derived inbred lines from the SBCC based on twenty-seven isolates of *B. graminis* f. sp. *hordei*.